HILGARDIA

A JOURNAL OF AGRICULTURAL SCIENCE

PUBLISHED BY THE

CALIFORNIA AGRICULTURAL EXPERIMENT STATION

VOL. 1 NOVEMBER, 1925 No. 12

SEX EXPRESSION IN SPINACH

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As would be expected in a dioecious, wind-pollinized plant, existing varieties of spinach are in general in a highly heterozygous condition. Commercial stocks are frequently of mixed varieties, of unsuitable types, or incorrectly named. These defects are the cause of much loss to growers and canners. Knowledge of the nature of the sexual conditions in spinach, as well as of the factors controlling sex expression, was considered essential to the work of plant breeding. There will be presented here, therefore, a description of the sexual conditions in spinach, together with results of certain experiments to test the relation of sex expression to ecological and physiological factors. The genetical aspects of sexuality in spinach will be dealt with in a later paper.

POSITION OF FLOWER CLUSTERS

After germination, spinach plants develop a rosette of eight or more leaves which arise from a much shortened stem (or "crown") located just above the surface of the ground and surmounting the thick, fleshy tap root. When the plant reaches a certain size, with the coöperation of favorable environmental conditions, the stem begins to elongate rapidly. At the same time, lateral branches arise from the axils of the rosette leaves, and in some varieties, these laterals may in time exceed the central stem in size and height. Secondary lateral branches arise from the leaf axils of both central and lateral stems. On these secondary branches, as well as on the upper portion of the central and lateral stems, are borne the flower clusters. These clusters are borne axially both on the larger stems and on the smaller branches arising from the same axils. Flowering usually begins on the middle portion of the larger stems and proceeds toward the base and the tip.

There are from six to twelve flowers in each cluster. These develop at such an unequal rate, however, that there are generally only two or three in bloom at once, and the flowering period of a single cluster extends over a period of from seven to ten days.

SEX ARRANGEMENTS IN SPINACH

With reference to the form of the mature plant, and to the distribution of sexes, spinach may be termed tetra-morphic. The four main classes of plants are: (1) "Extreme males." These bear only

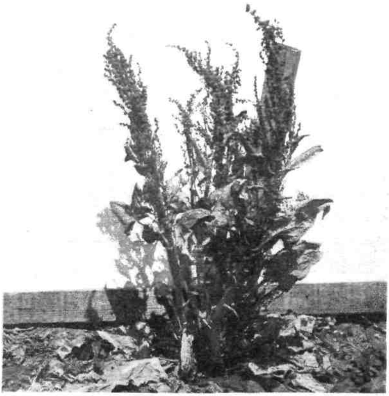

Fig. 1. "Extreme" type of male plant of Prickly Seeded spinach, in flower.

staminate flowers, and the leaves on the upper portion of the flowering branches are suppressed entirely or reduced to small scales. Representative plants of this type are shown in figures 1, 2, and 4. (2) "Vegetative males." These also bear only staminate flowers, but the leaves toward the tip of the flowering branches are more or less fully developed, as shown in figure 2. (3) Monoecious plants. These bear varying proportions of both staminate and pistillate flowers in the same cluster, and the leaves toward the tips of the flowering branches are fully developed. The ratio of staminate to pistillate flowers varies widely between the clusters on a given plant and between those on different plants. Thus a plant may be predominately

staminate, predominately pistillate, purely pistillate early in the season but with some staminate flowers later, or almost equally staminate and pistillate throughout the flowering period. The monoecious type is illustrated in figure 5. Rarely, one finds perfect flowers on monoecious plants. (4) "Female" plants. These bear only pistillate flowers and the leaves are fully developed to the tips

Fig. 2. Two types of male plants in the Long Standing variety. On right, extreme male. On left, vegetative male.

of the stems. Females of the Prickly Seeded variety are shown in figures 3 and 4. Other varieties do not differ materially.

Of the two kinds of male plants, the extreme type is by far the more common in nearly all strains of the Prickly Seeded variety that have been grown. In other varieties, the vegetative type of male is the more common. In the Long Season and similar varieties, practically all the males are of the vegetative type. The extreme males are the first to send up their seed stalks; in fact, they sometimes

do so without having formed any rosette leaves, thus producing the "spindle" type of plant figured by Kinney[8] and attributed by him to the effect of growing the plants in poor or unsuited soils. The writer's observations, however, indicate that this "spindle" condition is more probably connected with genetic factors, as is also the difference between the "extreme male" and the "vegetative male" type.

Fig. 3. Female spinach plant, in flower. When crowded the plants are taller and the development of lateral branches is less than here shown.

In 1924, a selected pistillate plant of the Prickly variety was pollinized by a vegetative male of another selection that produced males of that type only. The progeny in 1925 consisted of females and vegetative males. Strain No. 47 of the Prickly Seeded variety, which has been propagated for three years on the trial grounds of the Morse Seed Company at San Carlos, California, and has been rogued very carefully to remove all early flowering plants, now produces males of the vegetative type only, indicating that the early flowering extreme male character has been completely eliminated from the population. Commercial stocks of late or "long standing" varieties, which have been more or less carefully rogued to maintain the "long standing" character, produce few or no males of the extreme type. None of the treatments later described in this publication affected the proportion between the two types of males. All of these facts indicate that the

production of two types of male plants is due to genetic factors, and not to environmental influences.

Male plants, especially the extreme type, send up their stalks earlier, begin flowering earlier, and have a shorter flowering period than females. In the progeny of a strain that had been selected for uniformity of type for two years, records were kept of the date at

Fig. 4. Female spinach plant on left. Extreme male on right. Prickly Seeded variety.

which each plant in a row containing 234 plants began flowering. On the male plants the average date at which the first flowers of each stalk opened was April 25, while on the females it was May 6, two weeks later. Some of the male plants began to die on May 6, and the others were nearly through flowering. By May 13, pollen had become scarce in the field. All the "extreme" males were dead on May 25, though a few of the vegetative type survived. The female plants, on the other hand, were not all in flower until May 15, and they continued growing, flowering, and forming their fruits until June 10, when they were killed by Fusarium wilt and the heat. The significance to the commercial seed grower of this disparity in flowering period will be discussed in another paper. The early appearance of the flower stalks of the male plants leads to considerable loss to growers and canners.

While it is impossible definitely to identify male plants until after their stalks are well developed, it appears that in general the smaller and less vigorous individuals in the population are for the most part

males. Conversely, the plants that are larger in the early part of the season may usually be later identified as females. Thus, in 1923, 135 plants of various varieties were selected, chiefly because of their large size, early in the season. Of these, 72 per cent proved to be females and 28 per cent males. As will be seen later, this is not a normal sex ratio. In the same season, a row of Prickly No. 15 was thinned somewhat when the plants were half grown. Though this strain in other tests has produced regularly a slight excess of males, in this plot of 364 plants there were 46 per cent males and 56 per cent females. Apparently, where some thinning is practiced, more than half of the remaining plants are likely to be females, because in thinning, either either consciously or unconsciously, the workman removes the smaller, less thrifty plants, which it seems are to a large extent potential males. Apparently, in spinach the extreme male plants at least, are both biologically and horticulturally inferior to the females. The general differences in size, vigor, and duration of life for extreme male and for female spinach plants agree well with those reported by Schaffner[2] and McPhee[3] in the case of hemp. The vegetative males, however, have more nearly the form and the course of development of females. The development of strains in which all the males are of the "vegetative" type seems desirable, not only because of the elimination of the non-productive, early bolting "extreme males," but because the vegetative males more nearly coincide with the females in their flowering period, thus insuring more certain pollination.

Monoecious plants are relatively rare. In many strains, none have been observed. Smith[14] reports as many as 4 per cent in some strains. The highest proportion of monoecious plants observed in a commercial stock of spinach by the writer was in Long Standing No. 16, which in one plot of 162 plants, produced 52.5 per cent males, 38.8 per cent females, and 8.7 per cent monoecious plants. Thus it seems that the monoecious plants replace females in the sex ratio; i.e., the presence of such plants nearly compensates for an abnormal deficiency of females in the population. While monoecious plants in spinach are obviously inter-sexual in their nature, and occur in varying degrees of maleness or femaleness, still the occurrence of these intergrading forms has not been affected by the widely differing environmental conditions under which spinach plants have been grown. On the other hand, seeds from monoecious plants, which may or may not have been self-fertilized, produce progenies with an abnormally large proportion of monoecious plants. Thus, eight plants grown from a monoecious individual of the Savoy variety consisted of 1 female, 3 monoecious, and 4 male plants; and 39 plants grown from seed of

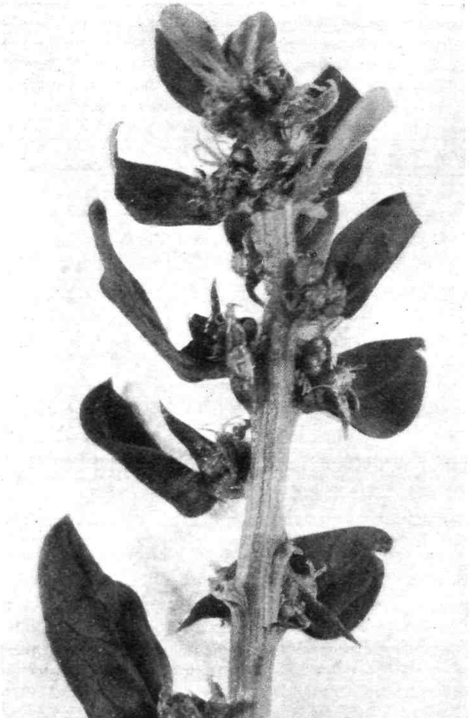

Fig. 5. Branch of monoecious spinach plant. Note the pistillate flowers and spiny seed in varying stages of development, and the anthers of staminate flowers.

a monoecious selection of the Long Standing variety consisted of 13 females, 7 monoecious, and 19 male plants. Another interesting point is that the monoecious plants in these two progenies presented the same degree of maleness or femaleness as did their respective parent plants—in one case predominately female, in the other predominately male. The evidence indicates that physiological conditions play no part in the occurence of intergrading sex forms in spinach.

There is, however, one phase of monoecism that may seem to be rather directly connected with physiological conditions within the

1 2 3 4 5

Fig. 6. Terminal branches from different types of spinach plants. (1) Extreme male, (2) an intergrading vegetative male, (3) vegetative-male, (4) monoecious, (5) female.

plant. In some strains, a considerable proportion of the plants, purely pistillate in the early part of their flowering period, produce late in the season, some staminate flowers toward the tips of the branches, especially of small lateral branches. Those who believe that sexuality of plants is determined in the somatic tissues by physiological influences may consider this a form of sex reversion associated with the declining vigor of the older plants and the more adverse conditions as to temperature and moisture supply to which the plants are exposed late in the season. A similar "end-season" sex change has been observed in other plants by several writers. However, the fact that this apparent sex reversion in spinach is limited to certain strains and to certain plants within these strains, while nearby plants under the same conditions continue to be purely pistillate to the end of the season indicate that this apparent sex reversion is connected with potentialities within

the plant based on genetic factors. It must always be remembered that spinach, being a wind-pollinized plant, produces in even the purest commercial strains, quite heterogeneous populations, consisting of plants with widely differing genetic constitution.

THE SEX RATIO IN DIOECIOUS PLANTS

The relation of physiological factors to sex-expression has been extensively investigated in dioecious plants, though our knowledge for the basis of sex in plants is at present in a rather confused state. Much of the work reported to date indicates the possibility of physiological control of sex in plants. Thus, Halstead[6] states that in hemp grown on heavily manured soil, there was an excess of pistillate plants, while on the adjoining unmanured plot there was nearly a 1:1 ratio. Shaded, irrigated, and check plots also produced the two forms in nearly 1:1 ratio. Halstead also grew hemp from early, medium, and late maturing seed and observed a slight tendency for an increasing proportion of females in populations grown from the medium and late matured seed.

Correns[2] studied the effect of environmental conditions upon the ratio of hermaphroditic and pistillate flowers produced from day to day on the gyno-monoecious plants of *Satureja hortensis*. He observed an apparent connection between poor nutrition (due to poor soil, deficient light, or disadvantageous position of the plant) and a decreased proportion of hermaphroditic flowers. Under favorable growing conditions, there were only 13 per cent hermaphroditic flowers, as compared to 79 per cent under normal conditions of culture. He also observed that different strains of *Satureja hortensis* showed marked differences in the percentage of perfect and pistillate flowers. Later, Correns[3] reports that in a dioecious species of *Melanthium* there were approximately 44 per cent male and 56 per cent female plants. The sex ratio was said to be affected by varying the amount of pollen applied to the pistillate flowers. With a superabundance of pollen, 12 per cent more females were produced by the resultant seeds than from flowers receiving only a small amount of pollen. Cutting off the style soon after pollination also increased the per cent of females, indicating that female-producing pollen grains may have a more vigorous pollen tube growth or in some way effect a more rapid fertilization of the ovules. Brambell[1] concluded that every fertilized ovum must contain the potentialities of both sexes, but in dioecious organisms the fertilized egg may contain a greater inherent tendency toward one sex than the other, the chances of reversal being inversely proportional to the differences in strength of the two tendencies.

Mercurialis annua has been a favorite species for the study of sex determination and of sex inheritance in plants. However, Gillot[5] questions the work of previous investigators with this plant, on account of the irregularity of germination of the seed. Seed collected in August, 1919, gave 14 per cent germination at once, 60 per cent in 1920, 55 per cent in 1921, 60 per cent in 1922, and 52 per cent in 1923. Apparently, the preponderance of one sex over another, in this plant, varies also with the season seeds are collected, for the ratio of males to females in collections made at different seasons by Gillot varied from 84:100 to 129:100. In spinach, commercial samples of which have from 15 to 50 per cent non-viable seed, this factor might be a cause of abnormal sex ratios, if there were any difference in the viability of male or female-producing seed.

Pritchard[10] was able to alter the sex of hemp plants by several different treatments, such as bagging the tops, injecting chemicals into the stem, and particularly by removing flowers. Reversal was secured in both directions; i.e., staminate plants were caused to form some pistillate flowers, and vice versa, leading to the conclusion that both males and females are potentially monoecious. Schaffner[13] found that hemp grown in the field during summer produced pure staminate and pistillate individuals in approximately 1:1 ratio, but grown in the greenhouse in winter, it evidenced great confusion in sexual expression. Both male and female plants appeared to have potentialities of both sexes, and Schaffner was led to conclude that reversal of the sexual state takes place in the vegetative tissues. McPhee[9] also found more inter-sex types in hemp when grown in the greenhouse in winter, but concluded that while "environment in some way affects the development of sex in this species, the evidence shows that it does not control it." Although McPhee grew the plants with controlled length of day, from 3 to 24 hours illumination, his report shows no connection between this factor and sex expression of the plants.

Schaffner[14] has been able to secure complete reversion of sex in *Arisaema*, in both directions, by altering the water and plant food supply. Dryness of the soil caused all the monoecious and most of the pistillate plants to change over to staminate form. Nearly all of these plants, as well as those originally staminate, became pistillate the following year, under the influence of heavy manuring and abundant moisture. This is probably the most complete and striking case on record of sex reversion in plants.

Reide[11] has studied the correlation between the sexual condition of plants and the quotient represented by the ratio of carbon assimilation

to absorption of inorganic salts. He finds that in corn this quotient must be higher for the development of pistillate than of staminate flowers. Gardner[4] concluded from the evidence in the literature that femaleness in plants is associated with rich soils, abundant moisture, liberal spacing, the vigor of youth, favorable growth conditions in general; maleness is associated with less favorable growth conditions. In his own experiments with a normally perfect-flowered variety of strawberry, Gardner observed changes in the sexual state, correlated with the widely differing nutritive conditions to which the plants were subjected. Nearly all plants "starved" by growing in sand expressed themselves as pistillate forms, while those grown in rich soil were normally hermaphroditic. This apparent contradiction to the general rule stated above, Gardner explained by the low carbohydrate content of the starved plants at the time of fruit-bud formation, a condition that is said to be more generally associated with extreme vegetative growth under the most favorable conditions.

The only mention* in the literature of sex ratios in spinach that has come to the writer's attention is the observation of Hoffman[7] that the ratio of males to females varies according to the spacing of the plants: when crowded or more or less stunted, males predominate; with wider spacing and better growing conditions there are relatively more females. No definite ratios are given. If the wider spacing was secured by hand thinning, however, then it is possible to explain the excess of females noted by Hoffman where the plants were widely spaced, for the operation of thinning, as has been previously mentioned, is likely to eliminate the least thrifty plants, the greater portion of which are potential males.

From the facts recorded in the literature, one can hardly escape the conclusion that no general rule can explain the phenomena of sex expression for all plants. In some plants sex may be more or less directly controlled by environmental factors; in others there is some apparent environmental control of sex expression, though the principal differences are determined genetically; and in still others there is no connection between physiological factors and sex; i.e., sex is controlled entirely by genetic factors. The following experiments indicate that spinach belongs to the last class.

* Recently, A. R. Zwaan (Seed World, **18**:6, 7–9, 1925) has stated that spinach seed grown in hot and dry climates produces an excess of male plants, while seed grown in the cool moist climate of Holland produces nearly equal number of males and females. However, tests of "place effect" are not reliable unless the different lots came originally from the same lot of seed. The writer's tests with California, Puget Sound, and Holland seed show no consistent relation of source to sex ratio.

EXPERIMENTS ON SEX EXPRESSION IN SPINACH

It was desired to determine whether sex expression in this plant could be influenced by environment, by nutritive conditions, or by other physiological means. The value to the seed grower, of any means of regulating the sex ratio, is obvious from the fact that yield of seed per acre depends largely on the number of female plants. Observations have been made on a large number of strains, including all commercial varieties grown in this country and in Europe, as well as in the progenies of some selections. Also plots have been grown to determine the effects of a single environmental factor on sex expresion. Seeds were sown rather thickly, no thinning was practiced, and the sex of every plant was recorded.

Nutritive Conditions.—Plants have been grown in parallel plots of poor sandy soil and of heavily manured soil during three different seasons. These plots were prepared in cold frames, though the plants were grown without cover. The sandy soil was poor enough to stunt greatly the plants grown in it. Those grown in rich soil were four to ten times as large. The results of the sex counts, taken as the plants began to bloom, are given in table 1.

TABLE 1

SEX RATIOS IN SPINACH GROWN UNDER DIFFERENT NUTRITIVE CONDITIONS

Variety	Date planted	Total No.	Per cent males	Per cent females	Per cent monoecious
Long Standing No. 11	Apr. 10, 1923				
Poor soil		46	48.0	50.0	2.0
Rich soil		32	47.0	53.0	0
Prickly No. 38	Dec. 3, 1923				
Poor soil		75	46.6	53.4	0
Rich soil		121	46.3	53.7	0
Prickly No. 15	Feb. 25, 1924				
Poor soil		115	54.8	45.2	0
Rich soil		85	58.8	41.2	0
Prickly Sel. No. 10	Jan. 20, 1925				
Poor soil		190	48.4	50.6	1.0
Rich soil		202	55.0	45.0	0
Total for all tests:					
Poor soil		426	49.8	49.5	0.7
Rich soil		440	49.8	50.2	0

The combined results for all the tests being considered, it appears that there is almost exactly a 1:1 ratio between males and females. Fortunately, there were practically no monoecious plants to confuse the results. However, in the individual tests, the ratios varied slightly,

a fact which may be due to a tendency for certain strains to produce more of one sex than the other, though the numbers of plants in the individual tests were hardly great enough for such small departures from the 1:1 ratio to be significant.

Shading.—Parallel plots of spinach were grown for three years, one plot being covered by unbleached "CC" muslin supported on a frame 3 feet high, the other being left uncovered. Marked differences in the size, form, and rate of growth of the plants were noted. Plants in the shaded plots were lower in per cent of dry matter, and sent up stalks and began to flower earlier. The results of the sex-counts are given in table 2.

TABLE 2

RELATION OF GROWING UNDER SHADE TO SEX EXPRESSION IN SPINACH

Variety	Date planted	Total No.	Per cent staminate	Per cent pistillate
Long Standing No. 11	May 15, 1923			
Under shade		75	48.0	52.0
Without shade		44	51.1	48.9
Prickly No. 15	Feb. 25, 1924			
Under shade		110	55.5	44.5
Without shade		90	57.8	42.2
Prickly Sel. No. 10	Jan. 20, 1925			
Under shade		197	48.2	51.8
Without shade		195	55.3	44.7
Totals:				
Under shade		382	50.5	49.5
Without shade		329	55.6	44.4

On the whole, plants grown under shade produced almost exactly a 1:1 ratio of males and females. The unshaded plants produced a slight excess of males in each case. Prickly No. 15 is a California-grown stock, extremely heterogeneous in type and the seed was of low viability. Prickly Selection No. 10 is a California-grown stock of very low viability, selected for two years for uniformity and for the long standing habit. It is the latter strain that is of special interest here for the same stock was used in other tests involving a larger number of plants and in each case produced as many or more males than females. May it be that certain strains produce seed which carry the factor for one sex to a greater extent than the other?

In any case, it seems that shading had little or no effect on sex expression, in spite of its marked effects upon the physiological activities of the plants and probably upon the chemical composition.

Spacing.—The amount of space a plant has in which to develop affects its form and activities. As compared to plants with ample room,

crowded spinach plants elongate the central stem earlier, and in fact, may form no crown and rosette leaves at all; the internodes and leaf petioles are longer; axillary branches are mostly or entirely suppressed; and the flowering period begins earlier. This agrees with the commonly known fact that conditions of culture may cause quite as much difference in the form of a plant as do hereditary factors. The possible effect of plant spacing on the sex ratio was also studied. Rows were sown at the standard width of 15 inches, but with varying amounts of seed, so as to minimize the necessity for thinning to secure the desired spacing. That thinning tends to eliminate a greater number of males than of females, and so upsets the normal sex ratio, has already been mentioned. Table 3 gives the results of the more detailed experiments on spacing.

TABLE 3

RELATION OF SPACE IN THE ROW TO SEX EXPRESSION IN SPINACH

Variety	Date planted	Total No.	Per cent staminate	Per cent pistillate	Per cent monoecious
Prickly No. 38:	Dec. 10, 1923				
6″ apart		330	48.2	51.8	0
2″ apart		689	50.5	49.5	0
1″ apart		645	50.4	49.4	0.2
Prickly No. 72	Feb. 19, 1925				
3″ apart		130	46.9	53.1	0
1″ apart		243	43.2	56.8	0
Prickly No. 73	Feb. 19, 1925				
3″ apart		72	48.6	48.6	2.8
1″ apart		135	45.9	54.1	0

In the spacing tests with Prickly No. 38, where large numbers were involved, almost exactly a 1:1 ratio was produced in the 1 and 2 inch spacings where practically no thinning was done. To secure the 6 inch spacing, some thinning was necessary, and here there was a slight preponderance of females. Prickly No. 72 and No. 73 proved to be stocks of identically the same strain, though secured from different sources. With this strain there was a slight though consistent excess of females, regardless of spacing, the opposite of a condition that has already been pointed out in two other strains. It appears that spacing does not affect the sex ratio in any case.

Date of Planting.—It was thought that the relation of length of day to sex expression could be studied through plantings made at intervals in winter and spring. However, it was found that the different winter plantings flowered at nearly the same time, while

plantings after March 1 perished from the heat before flowering. Nevertheless, time of planting (early or late winter) does affect the vegetative development of the plants very materially. In California, November and December plantings develop very slowly during the cold weather, but grow rapidly during the warm moist periods of late winter and early spring. January and February plantings grow rapidly from the start, but do not attain as large size before stem elongation and the reproductive processes begin. The plants in a plot of Prickly Selection No. 10, sown November 15, began to flower during the period April 14 to May 14. The same strain sowed February 2, began flowering from May 1 to May 24. Nine weeks difference in planting resulted in only two weeks difference in flowering. One row of the November planting, which contained 234 plants, produced 58.6 per cent males and 41.4 per cent females. Another row planted on the same date and containing 310 plants, produced 57.1 per cent males and 42.9 per cent females. In the February planting, there were 266 plants, of which 52 per cent were males and 48 per cent females. The tendency of this strain to produce an excess of male plants has already been mentioned. The date of planting does not seem to have altered the sex ratio materially.

Mutilation.—Ten male plants that were about to flower were cut back to stubs on May 1. The small axillary branches that were left developed and produced an abundance of staminate flowers only. Ten female plants that had just begun flowering were likewise cut back. Branches that subsequently developed on these plants produced only pistillate flowers.

CONCLUSIONS

Spinach is tetra-morphic, though there are intergrading forms in the purely staminate and in the monoecious classes.

Environmental influences seem to have no effect in determining which type shall be developed. In the case of the two types of males, and in the monoecious forms, there is evidence that the differences are due to genetic factors.

Male plants, especially the "extreme males," are in general smaller, form flower stalks earlier, bloom earlier, and die earlier than female plants.

In general there is a 1:1 ratio between male and female plants, but some strains seem consistently to produce a slight excess of male plants, while others of the same variety produce an excess of females. This fact, if borne out by further tests, may be utilized through plant-breeding methods to the advantage of the seed grower, who would prefer to have an excess of females in the population.

Experiments to test the influence of rich versus poor soils, of shade versus full light, of wide versus close spacing, of early versus late planting, and of mutilation, have shown that none of these treatments have any appreciable influence on sex expression in spinach.

Thinning is the only cultural treatment affecting the sex ratio in spinach that is likely to be of any value for the seed grower. If the seeds are sown thickly and the smaller plants are rogued out early in the season, those remaining may present an excess of females.

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